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GEOCHEMICAL ACTIVITY OF SOIL MICROORGANISMS AS AN INTEGRAL PART OF BIOGEOCENOSIS

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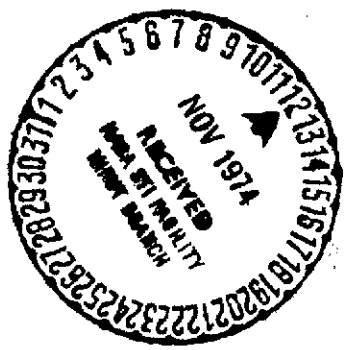

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16. Abstract

A review with 30 references discussing clay minerals and organic matter decomposition and transformation by soil microorga-isms, the effect of hydrothermal and other factors on this microbial activity, and the effect of microbial activity on chemical processes in soil and on soil formation.

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GEOCHEMICAL ACTIVITY OF SOIL MICROORGANISMS AS AN INTEGRAL PART OF BIOGEOCENOSIS

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T. V. Aristovskaya

In studying soil microflora from the biogenocenotic point of view, most attention is directed toward determining the count and the qualitative composition of microorganisms, investigating the rhizosphere effect, and examining the role of microorganisms in the decomposition of organic debris entering the soil and in the fixation of atmospheric nitrogen. The vital activity of fungi, bacteria, and actinomycetes as components of biogenocenosis is examined chiefly from the viewpoint of its role in the mineralization of the organic matter produced by plants. Microorganisms figure predominantly as heterotrophes, whose main planetary function consists in returning carbon assimilated by green plants to its initial state, and as suppliers of the bound nitrogen essential to plants.

These processes attract the greatest attention of investigators probably for several reasons. First, their significance in the biosphere is unquestioned; second, the participation of microorganisms in these processes has long been proven; and, third, this aspect of the biochemical activity of the microflora is the most easily demonstrated and accessible to investigation. Without denying the enormous significance of microorganisms providing the most vital links in the recycling of nitrogen and carbon in the biosphere, we wish to dwell on another, no less important, aspect of their biogeochemical activity.

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It is important that essential to the existence and flourishing of biogeocenosis is not only the fixation of the mineral forms of nitrogen and carbon, their conversion to organic compounds, and the subsequent mineralization of organic debris. Life requires the assimilation, transformation, and movement of nearly all

chemical elements present in the earth's crust. Without involving in biological recycling phosphorus, potassium, sulfur, calcium, manganese, iron, and so on, vital activity of neither animals, plants, nor microorganisms is possible.

In examining the recycling of substances in well-developed soils intrinsic to stable biogenocenoses, very often we represent to ourselves in simplified fashion the fate of mineral elements in this recycling, assuming that the cycle of their transformations reduces only to three main processes: processes of absorption of the elements of high-ash nutrition by the higher plants from the soil in the form of mineral salts, their incorporation in the composition of plant tissues, and their return to the soil together with plant remains for subsequent mineralization.

It would be naive to believe that the transformation cycles occurring in biogeocenoses actually fit into this simple scheme. Under this treatment of the process, the mineral part of soil would appear to be entirely divorced from its living organic part and would not be involved as a participant in recycling. Assigned to the mineral mass of soil is virtually the role of an inert substrate within which processes of the building and breakdown of organic matter by living organisms go on.

But in reality, in all biogeocenoses without exception, also entering into the recycling of mineral elements are processes of the profound transformation by living organisms of the material of soil-forming rocks. During these processes minerals are broken down and formed anew, new portions of inert matter are brought into the sphere of life, and there is a temporary passing from recycling of stable chemical compounds produced by living organisms. The significance of these processes for the existence and development of biogeocenoses is of course enormous.

Minerals of soil-forming rocks are the primary sources of ash nutrition for all living creatures on land. But the possibility

of their assimilation is realized by life predominantly as the result of the biochemical activity of microorganisms during the soil-forming process. When rocks are broken down, the requirements of all living components of biogeocenoses for the elements of mineral nutrition are met. This is manifested most graphically in the biogeocenoses corresponding to the early stages of soil formation when accessible forms of high-ash substances have not yet accumulated and the minerals of soil-forming rocks are essential their only or almost only source. This process is vitally essential also in biogeocenoses formed in conditions of a humid climate where the systematic removal of all soluble chemical compounds beyond the bounds of the biogeocenosis is possible, and where these losses must be continuously compensated in some way.

Unfortunately, thus far the conversion of minerals in developed soils has been studied predominantly not by biologists, but by soil scientists and mostly from purely mineralogical or chemical vantage points. The place of the biochemical activity of microorganisms here in most cases is wholly ignored. But nonetheless, modern geological microbiology has accumulated experimental data confirming the enormous role of microorganisms in the transformation of rocks and in their formation and breakdown (Pomerants and Belenitskaya, 1969; Lyalikova and Shlain, 1969, and others). /13

The results of studying the geological activity of microorganisms not only expand our ideas of the scales of the planetary work done by microorganisms, but are also utilized in practice. In particular, the cultures of certain species of Thiobacillus and Ferrobacillus are used for leaching valuable elements (copper, uranium, and so on) from low-grade ores in the mining industry, since the microbiological method of treatment proves to be much more effective and economically advantageous than the chemical method (Ehrlich, Fox, and Sally, 1967; MacGregor, 1969, and others). All these facts must be taken into account when investigating the microbial component of dry-land biogeocenoses.

Relying on the data accumulated by science, let us examine the least-studied links in the recycling of mineral elements in soils -- the processes of decomposition and formation of minerals by microorganisms.

Based on information available in the literature and the results of our previous work (Aristovskaya, 1965; Aristovskaya, Daragan, Zykina, and Kutuzova, 1969), it can be concluded that the vital activity of microorganisms plays an enormous role in the transformation of the mineral part of soil, and above all can be both the direct and indirect cause of the breakdown of the crystal lattices of minerals and the conversion of their constituent chemical elements into a state that is active and accessible to plants.

An example of the direct action can be the breakdown of minerals with the aid of microbial enzymes or the extracellular minerals formed by microorganisms and deposited on the surfaces of their cells in the form of slimes. The decomposition evidently of only a few minerals proceeds enzymatically, and this mechanism cannot be regarded as the predominant pathway for the mobilization of the chemical elements from stable natural inorganic compounds. At the present time, there are known to be enzymatic reactions leading to the breakdown principally of minerals that include sulfur or iron in their composition. These elements under the effect of the appropriate enzymes are oxidized or reduced, which then leads ultimately to the breakdown of the mineral. In this fashion, in particular, proceeds the disintegration of pyrite, chalcopyrite, covellite, and several other sulfide minerals by certain representatives of the genera Thiobacillus and Ferrobacillus capable of utilizing the energy released through the oxidation of sulfur and divalent iron (Silverman and Melvin, 1967; Lyalikova, 1970; Ehrlich, 1971). For the oxidation reaction to be carried out requires direct contact of microbial cells with the mineral

surface (Silverman and Melvin, 1967). Actively metabolizing bacterial cells in this case are firmly secured to the particles of the corresponding minerals (Ehrlich, 1971).

Enzymatic breakdown of minerals containing trivalent iron occurs when the latter is utilized by microorganisms (in anaerobic conditions) in place of free oxygen, as an oxidizer (Bromfield, 1954; Duda and Kalakutskiy, 1961; Aristovskaya, 1965; Ottow, 1968; Aristovskaya, Daragan, Zykina, and Kutuzova, 1969; Aristovskaya and Zavarsin, 1971). As a result of this process, the valency state of iron changes and it converts to the divalent form, thus acquiring greater mobility.

In addition to enzymes, microbial slimes also have a direct effect on minerals of soil-forming rock (Vinogradov and Boychenko, 1942; Tesic and Thodorovic, 1952; Claus, Wittman, and Rippel-Baldes, 1958), consisting for the large part of extracellular polysaccharides containing uronic acids (Claus, Wittman, and Rippel-Baldes, 1958). /14 The carboxyl and phenol groups present in the composition of slimes react with the elements incorporated in minerals, forming with them complex compounds. As a result of this interaction, a mineral is disintegrated and its constituent chemical elements pass into solution.

It can be assumed that slime formation is of more significance in this process than the enzymatic activity of the corresponding microorganisms, since the action of slimes on rock is less specific in character than the action of enzymes. Slime formation is a fairly widespread phenomenon in soil conditions. From available data (Finch, Hayes, and Stacey, 1971), most of the polymers found in soil are of microbial origin and represent extracellular polysaccharides and polyuronides of microorganisms, in other words, microbial slimes and their residues.

When the microbial landscape of various soils is studied with capillary pedoscopes, we not infrequently detect large

numbers of microbial cells surrounded by slime capsules, which is in agreement with what has just been said.

In spite of the broad distribution among microorganisms of the ability to form slime, evidently the most widespread and efficient method of extracting mineral nutrition from soil-forming rock is the indirect action on it of microorganisms, that is, the disintegration of rock by means of metabolites produced by the microflora.

Among the metabolic products excreted into the ambient environment by microorganisms very strong chemical reagents are to be found. They include various mineral and organic acids, biogenic alkalies, chelating agents, and compounds with strong reducing properties. Of the mineral acids produced by microorganisms, primarily noteworthy are such strong acids as nitric acid, a metabolite of nitrifying bacteria, and sulfuric acid, formed by bacteria oxidizing compounds of sulfur.

Worthy of note is the amazing fact that some species of sulfur bacteria are capable of developing at very low pH values and accumulating sulfuric acid in a concentration corresponding to its 10 percent solution; here the pH of the medium falls below 1.0 under the effect of their vital activity (Poshon and Barzhak, 1960). Sulfuric acid at this concentration is capable of burning a sheet of paper or cotton cloth; naturally, minerals of soil-forming rock are gradually broken down under its influence. Wagner and Schwartz (1967 a and b) showed that under the effect of the culture Thiobacillus thiooxidans, forming sulfuric acid, very intensive breakdown of certain aluminosilicates takes place, which with time leads to the complete dissolution of all their constituent chemical elements.

The extraction of nutrients from minerals by means of inorganic acids can be of high significance at the early stages of soil formation and of the formation of a biogeocenosis, when the

primary production of the community is still low and among its constituents species of bacteria with the autotropic type of metabolism figuresprominently (nitrifiers and sulfur bacteria). In stable biogeocenoses with a high production of organic matter, especially in communities formed in humid climatic conditions, there are the prerequisites for the formation (during the mineralization of vegetative fall) of large amounts of the most diverse organic acids, beginning with the simple, low-molecular and ending /15 with specific, humic acids. An appreciable accumulation of mineral acids (especially, nitric) in soils with elution conditions is improbable (Aristovskaya, 1965).

The ability to form acids is widespread in the world of microorganisms and doubtless plays a vast role in providing communities with elements of mineral nutrition through the breakdown of the material of soil-forming rocks. Among the organic acids produced by microorganisms there are compounds exhibiting not only acidic properties, but also at the same time the ability to form chelates. This enhances their corrosiveness with respect to soil minerals and is responsible for the varied character of their possible interaction with the latter.

Work by Duff, Webley, and Scott, 1963, and others) established the fact that natural phosphates and silicates dissolve under the effect of 2-ketogluconic acid released by bacteria, by forming complex compounds with certain divalent metals, including Ca, Cu, and Mn. Similar data were obtained by Nyberg et al. (cited in Duff, Webley, and Scott, 1963) for 3-phosphoroglyceric acid. Wagner (1966) places high significance in weathering on oxalic acid formed by fungi and bacteria in soils.

Schatz et al. (Schatz, A., Cheronis, Schatz, V., and Trelawny, 1954) pointed out that soil formation proceeds not only in an acid but also in a neutral or alkaline medium. Accordingly, they believe that in some cases chelation can be the most important factor /

of weathering. The release by organisms of organic complexating agents, in their view, has high adaptive significance when an organism exists in a medium where the elements of mineral nutrition are in an undissolved form. In several cases this type of microbial metabolite has antibiotic properties. The authors maintain that this provides for the competitiveness of these species in their struggle for mineral nutrition.

Microorganisms producing organic acids and compounds capable of complexation thus prove to be very important constituents of a biogeocenosis by furning the members of the community with mineral nutrition. In several cases all the vitally essential elements extracted from a particular mineral initially are consumed by the microorganism -- the producer of the chemical compounds breaking down the rock and only after its death do these chemical elements become available to other micro- and macroorganisms.

This phenomenon was found by us (Aristovskaya, Daragan, Zykina, and Kutuzova, 1969) in the decomposition of nephelin by a culture of pseudomonad exhibiting the ability of both acid formation and slime formation simultaneously. Developing on pieces of the mineral, these bacteria are responsible for a significant breakdown of the latter and the passing into solution of appreciable amounts of silicon, aluminum, and in part, sodium. But the potassium extracted from nephenlin in certain conditions is wholly retained by the microbial cells consuming it.

A completely different picture is observed in the breakdown of the very same mineral by a culture of Penicillium notatum. A film of the fungus develops on the surface of the liquid medium and does not come into direct contact with the nephelin particles. Nonetheless, the breakdown of the mineral under the effect of the acids produced by the fungus occurs with such an intensity that Penicillium notatum does not utilize all of the potassium cations it liberates and much of the potassium accumulates in the medium.

Therefore, some microorganisms are capable of providing mineral nutrition not only for their requirements, but at the same time to some extent for the needs of other members of the community.

Interesting patterns of interactions among various species of bacteria involving the extraction of essential nutrient elements from minerals have been found by Wagner and Schwartz (1967 a and b) in studying processes of the decomposition of certain aluminosilicates by microorganisms.

Slime-forming bacteria, by attacking particles of a mineral, develop on its surfaces in the form of a continuous film. But associated bacteria are concentrated in immediate proximity to their microbial slime formers overgrowing the mineral particles; in the authors' view, this affords grounds for assuming mutually advantageous relationships between the corresponding species of microorganisms. Similar ties probably can exist between higher plants and certain constituents of rhizosphere microflora.

While acids and compounds produced by microorganisms and capable of forming chelates can be evaluated as the most important agents in the transformation of the mineral portion of soil, the role of biogenic alkalies in weathering processes is still poorly studied. According to available data (Aristovskaya, Daragan, Zykina, and Kutuzova, 1969; Kutuzova, 1970), the vital activity of alkali-forming bacteria, in particular, aluminifiers, has a certain effect on some soil minerals and significantly promotes the breakdown of the strongest of these minerals -- quartz.

In biogeocenoses formed in conditions of intense waterlogging and characterized by considerable development of anaerobic processes, an essential role in the breakdown of certain minerals is evidently played by microorganisms forming in their vital activity various compounds that are strong reducing agents: hydrogen, hydrogen sulfide, methane, and so on. Under the effect of biogenic reducing agents, the oxide forms of iron and manganese can be reduced

and as a result, the breakdown of minerals containing the elements listed in their crystal lattices can take place.

Depending on the action of which particular microorganisms the breakdown of minerals takes place, the results of this process can differ. In some cases the gradual complete dissolution of the mineral is possible, as was observed by Wagner and Schwartz (1967), and by R. S. Kutuzova (1970) in experiments on nephelin. Under the effect of certain heterotrophic bacteria and their metabolic products, it is not the complete breakdown of a mineral that may occur, but a gradual change in its chemical composition, which -- with time -- must lead to its transformation into another mineral. In microbiological literature can be found data proving that when microorganisms act on aluminosilicates, alkali elements are the first to acquire mobility, followed by the alkaline-earth elements, and lastly, silicon and aluminum (Wagner and Schwartz, 1967 a and b; Aristovskaya, Daragan, Zykina, and Kutuzova, 1969). Interestingly enough, some microorganisms are responsible for the predominant accumulation of aluminum in the mineral residue of the decomposing aluminosilicate, and others cause the predominant accumulation of silicon. It is probable that this is associated with the differences in the mechanism of the chemical action of various species on a mineral. A similar phenomenon was discovered by J. Pedro (1971) in studying the decomposition of minerals under the effect of various chemical reagents.

By simulating hydrothermal conditions characteristic of the tropical zone, the author used as chemical agents of weathering carbon dioxide, hydrogen sulfide and acetic acid. The objects for the action of these compounds were granite and basalt. It was found that the direction of weathering depends not only on the chemical composition of the rock, but also on the nature of the chemical compound acting on it.

At the same temperature and hydrodynamic conditions, under the effect of carbonate, hydrogenssulfide, and acetic acid water the relative removal of SiO_2 and Al_2O_3 was found to differ. In experiments with CO_2 and H_2S, the intensive leaching of SiO_2 /17 from the decomposing material and the relative accumulation in it of Al_2O_3 were observed. But the treatment of rock with a solution of acetic acid led to the opposite results, and the dissolution of aluminum occurred much more vigorously than the removal of silica. The author assumed that in the latter case during the decomposition of the basalt ultimately the complete removal of aluminum from the initial rock and the relative accumulation therein of silica must have occurred. Ultimately, the solid residue at the last decomposition stage must consist of only silica. In the author's view, this type of weathering is close to the process of podzolization.

In evaluating the results of this interesting experiment of Pedro, it must be borne in mind that all the chemical compounds he used are the products of vital activity, and in particular are metabolites of various microorganisms. This author's data confirm our concept that the weathering of soil minerals occurring under the direct or indirect action of microorganisms with different types of metabolism proceeds differently and sometimes leads to directly opposite results.

All the foregoing illustrates the vast role of soil microorganisms in the links of the biological recycling of mineral substances in biogeocenoses that provide for the mobilization of the corresponding nutrient elements from stable chemical compounds and the involvement in the sphere of life of material from soil-forming rocks. These processes doubtless are of vast significance for all living components of a community and influence the formation of a biogeocenosis as a whole.

No lesser a role is played by the vital activity of microorganisms also in the withdrawal of corresponding chemical elements from recycling that occurs, in particular, during biogenic mineral formation. This process leads to a considerable change in the habitat conditions of all soil-associated organisms and, doubtless, is reflected in the functioning of the biogeocenosis. Under the effect of the neoformation of clay minerals, for example, the absorptivity of the soil must increase, and changes must occur in its mechanical composition, its structure and filtering ability, and also in the type of organomineral compounds predominant in it.

The participation of microorganisms in the neoformation of minerals has as yet been poorly studied. Until recently, this problem was the object of investigation mainly by microbiologists working in the field of geological microbiology, and accordingly, minerals of practical interest to the mining industry were the ones chiefly studied.

T. V. Voytkevich et al. (1968) showed that pyrite formed through the interaction of the metabolic products of sulfate-reducing bacteria and microorganisms reducing oxide iron.

In this case, the emergence of a new mineral occurs with the indirect participation of microorganisms through chemical reactions between their metabolic products. However, in the absence of microflora these processes would be impossible.

Mineral formation can be not only an indirect, but also a direct consequence of the vital activity of microorganisms. In particular, through the biochemical activity of iron-manganese bacteria the hydroxides of iron and manganese intensively accumulate in the bulk of several kinds of soils and at the bottom of ore-bearing lakes. With the course of time, bacterial colonies covered with ferruginous or iron-manganese deposits can be converted into concretions (Aristovskaya, 1965; Dubinina, 1970), and on being gradually crystallized, they acquire the properties

of minerals. Both autotrophic as well as heterotrophic microorganisms can participate in the accumulation of iron, and the actual process of the accumulation of this element is the consequence either of the oxidation of its ferrous forms into the oxide, or the mineralization of the organoiron compounds of the corresponding microflora. The investigation we conducted of the structure of soil micro-ortsteins (Aristovskaya, 1965) showed that these formations are nothing other than microbial colonies covered with ferruginous and iron-manganese deposits. /18

D. R. Gabe and A. M. Gal'perina (1964) showed that the formation of iron-manganese interlayers in oozes proceeds only when specific microflora is present, while in sterile conditions the process stops altogether. G. A. Dubinina (1970) was able to obtain microconcretions experimentally in the conditions of a laboratory experiment with bacterial cultures.

In spite of the fact that the ability of microorganisms to accumulate iron and manganese is an irrefutable fact, the biological conception of ore formation has not yet won universal recognition. Evidently, not only must the fact of the ability of microorganisms to accumulate these elements be demonstrated, but also their predominant role in ore formation in nature.

In 1947 an article by A. G. Vologdin was published, presenting the findings of a microscopic examination of various ores by the polished section method. In all the objects studied were found structures similar externally to bacterial cells. The author concluded that all the ores he investigated are the result of the vital activity of microorganisms. The Vologdina hypothesis was rejected by geologists as completely unsubstantiated, which in part can be accounted for by the unreadiness of the geological community to accept these ideas. But the main reasons was, as it appears to us, the blurred quality of the microphotographs presented by the author and the inadequate study at that time of the

flora of iron bacteria. Many of the now-known representatives of this group had not yet been described in the 1940's and therefore the microbial-like structures detected by the author did not have living analogs sufficiently similar morphologically. During the period elapsing since the publication of Vologdin's study much additional information has accumulated confirming the biological theory of ore formation and we deemed it expedient to conduct similar observations with the aid of microbiological methods. We used as objects of our investigation two samples of limonite, two samples of goethite, and one sample of magnetite obtained from the Museum of the Leningrad Mining Institute. The limonite and the goethite are formed, as is known in the weathering crust, and this affords grounds for assuming that it is possible that they were formed through the biochemical activity of iron bacteria. Magnetite was taken for comparison as a mineral of clearly nonbiological origin.

Pieces of the minerals studied were broken into several parts and the silts obtained from the fracture surface by rubbing two pieces against each other was subjected to study. The silt was placed on an object slide and subjected to microscopic examination with maximum magnification of the light microscope, initially without any preliminary treatment, and then after partial dissolution of the iron oxides with an oxalic acid solution and staining of the preparation with carbolic erythrosine. In addition to the usual microscopy, crossed-Nicol microscopy was carried out to verify the crystalline nature of the objects studied.

The results of the investigations are given in the microphotographs (Figs. 1 and 2). Photographs 1 a and b show a piece of goethite photographed in different conditions of microscopy and not subjected to any preliminary treatment. In the photograph can be seen the outlines of cells of iron bacteria and their connective filaments, covered with ferruginous deposits. Photograph 1 b taken in crossed Nicols clearly shows that we are

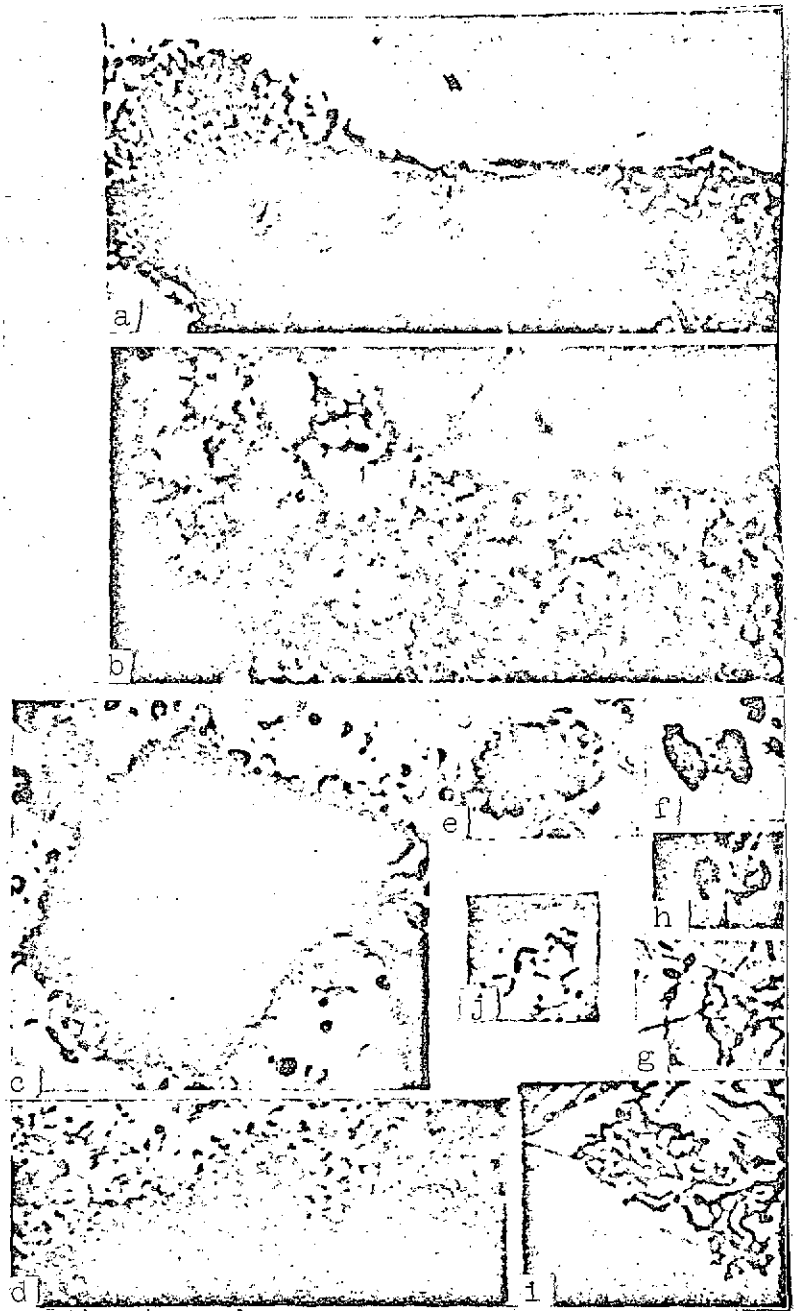

Fig. 1. Microstructures of samples of goethite and limonite similar to the structures of colonies of Pedomicrobium, power 1000 (10x60)

a. goethite particle

b. same particle photographed in crossed Nicols /caption concluded on next page/

c, d, e. particle of goethite after treatment with oxalic

/Caption to Fig. 1, concluded/

acid and stained with erythrosine

f. particle of limonite treated with oxalic acid and stained with erythrosine

g, h. section of photograph of culture of Pedomicrobium taken from a paper by Hirsch (1968). Cells and filaments of the organism are covered with deposits of iron hydroxide

i, j. the same organism without ferruginous deposits

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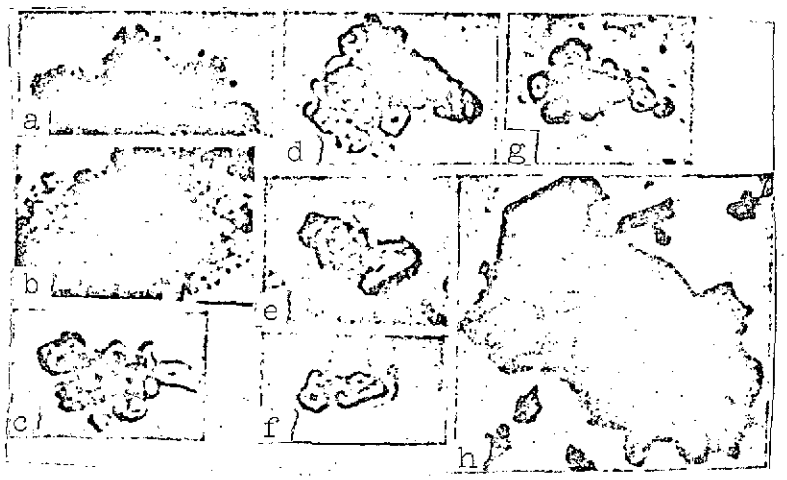

Fig. 2. Microstructures of samples of goethite, limonite, and magnetite, power 1000 (10x60)

a, b. particles of goethite treated with oxalic acid and stained with erythrosine

c, d, e, f. particles of limonite treated with oxalic acid and stained

h. cells of Siderocapsae culture

i. particles of magnetite

dealing not with an ordinary microbial colony covered with ferruginous deposits, but with a crystallized body.

Cellular structures are seen even more distinctly in photographs of goethite and limonite preparations (Fig. 1 c, d, e, f) treated with oxalic acid and stained with erythrosine. Using a micrometer screw in the microscopic examination of these objects, it is not difficult to see that practically the entire mineral particle consists of thick ferruginous deposits, copying the contours of the microbial bodies enveloped therein. In the photographs this is not so distinctly evident since the various sections of each mineral particle are of different thicknesses and this severely hinders the focussing of the microscope during photography. By comparing the microscopic structure of the minerals with the growth forms of iron-manganese bacteria in pure or mixed cultures, one can detect certain features of similarity between the remains of the microorganisms forming the samples of goethite and limonite studied, and fragments of colonies of certain present-day bacteria. In particular, the goethite sample shown in the figure (1, a, b, c, d, e, f) consists of mineralized overgrowths of some microorganism with a cellular-filament structure type, characteristic of representatives of Hyphomicrobiales. Belonging to the same bacterial group is Pedomicrobium; the photographs of this genus (see Fig. 1 g-k) were taken from an article by Hirsch (1968) dealing with a pure culture of this organism.

The other goethite sample also disclosed remains of microorganisms with a mycelial structure of colonies (Fig. 2 a and b), but judging from the shape of the latter and the cell dimensions, they were formed mainly by other species of iron-manganese bacteria.

One of the limonite samples investigated consisted of remains of ferruginized colonies of an organism (Fig. 2 c-f) morphologically very similar to Siderocapsae, whose cells are shown in Fig. 2 h). In the other limonite sample there was a predominance of hyphomicrobial bacterial forms. Bacteria from the limonite sample were readily stained with erythrosine (Fig. 2 d, e).

The results of these observations not only confirm the biological origin of the minerals studied, but also make it possible to approximately determine which groups of microorganisms participate in the process of their formation. /21

The magnetite silt differs sharply from the minerals just examined by the complete absence in it of any similarity to cellular structures (Fig. 2 1).

All this provides grounds for suggesting that the formation of goethite and limonite in the weathering crust occurs through the vital activity of microorganisms intensively accumulating iron. The hydroxide of this element accumulating around microbial cells is gradually dehydrated, subjected to crystallization, and transformed into a mineral. Since the forms of the iron hydroxide deposits repeat the contours of the microbial bodies immurred therein, the structure of the mineral long retains a similarity with the structure of the bacterial colony, analogous to how a gypsum mass preserves the features of the face of a deceased person. Some of the microbial cells immurred in the mineral deposits are converted into kinds of mummies and retain the ability to be stained with erythrosine throughout an indefinitely long period of time.

All the foregoing shows that microorganisms are a special force capable of causing the greatest chemical transformations on the earth's surface.

The scales of their geochemical activity in the transforming of mineral elements in the earth's crust are wholly commensurable with the scales of the processes of mineralization of organic remains and the fixation of atmospheric nitrogen in the biosphere that they carry out. Through the ability of microorganisms to cause the most diverse chemical processes, their vital activity is the most important medium-forming factor in biogeocenoses. This is promoted not only by the diversity and high activity of microbial enzymes, but also by the uniqueness of metabolism inherent in microorganisms.

In contrast to higher plants and animals in which all metabolic reactions (with rare exceptions) proceed within their organs and tissues, microorganisms are capable of carrying out the conversion of their energy and nutrition source outside the cell. Animals and plants release into their ambient environment predominantly the end products of metabolism, while in the case of microorganisms located outside the cell are not only the end, but also the intermediate products of metabolism, without losing their physiological significance for the microbe-producer. Let us clarify this with an example.

Carbon of cellular tissues or starch can be assimilated by bacteria only after the conversion of these polysaccharides into simpler soluble compounds capable of penetrating the cellular membrane into the cell. The first stages in the reworking of these substrates proceed in a medium by means of the exo-enzymes released by the bacteria. But into the cell comes not the primary source of carbon, but compounds formed at the intermediate stages of its transformation.

The biochemical agents available to microorganisms for extracellular conversion of substances include not only enzymes that have a specific action on certain substrates, but also microorganism-produced acids, alkalies, chelating agents, and other chemically active compounds. The role of the latter is especially large in extracting nutrient elements from the minerals of soil-forming rock.

As to significance for the vital activity of microorganisms, there is no fundamental difference between the action, for example, of extracellular amylase hydrolytically cleaving starch, and any acid or alkali releasing potassium or phosphorus from a soil-forming rock. In either case, the food sources are converted into a form more suitable for assimilation. /22

Utilization by the corresponding microorganism of the intermediate products of extracellular conversion of the substrate may be incomplete. Some of the compounds formed can accumulate in the medium or be consumed by other organisms.

Accordingly, the vital activity of microorganisms very strongly affects the chemical properties of soil. It reacts significantly to its pH and Eh, its content of accessible forms of nitrogen and mineral substances, provides for the formation of an unfavorable environment for the development of some species and promotes the flourishing of others, and so on.

Since the use of extracellular mechanisms for the reworking of nutrient and energy-providing substances is development in microorganisms very widely, in the study of soil processes it is very difficult to draw sharp boundaries between purely chemical and biological phenomena. Essentially, in soil there are no, or nearly no, chemical processes, but biogeochemical processes. Our investigations have led to these conclusions.

1. The recycling of mineral substances occurring in biogeocenoses includes processes of the profound transformation of the material of soil-forming rocks by microorganisms. During these processes, minerals undergo breakdown and neoformation, there is a continuous involvement in biological recycling of new portions of inert matter, and there is a temporary withdrawal from recycling of stable chemical compounds produced by living organisms.

2. The decomposition of minerals can occur under the effect of direct and indirect action of microorganisms on soil-forming rock. The agents of this action are microbial enzymes, bacterial slimes, and various metabolic products of microorganisms -- strong chemical reagents (mineral and organic acids, compounds capable of forming complexes with mineral elements, biogenic alkalies, and biogenic reducing agents).

3. Neoformation of minerals can also appear as the direct, as well as indirect result of the vital activity of soil microflora. In some cases the new mineral appears through the chemical interaction of two or more microbial metabolites with eachother, while in other cases, mineral formation is the immediate result of the vital activity of certain groups of microorganisms.

4. When the microstructure of several minerals was investigated, it was found that the samples of goethite and limonite studied are deposits of iron-manganese bacteria preserving the shape of the bacterial overgrowths and subjected to crystallization. This confirms the biological concept of mineralization.

5. The vital activity of microorganisms has an enormous effect on the chemical properties of soil and is an important habitat-forming factor in biogeocenoses.

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